Community dynamics: lessons from a skeleton

by

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Contents

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1 Abstract

Models describing the dynamics of complex ecological communities share one important component: a matrix describing which species interact with which others and how. The parameters of interaction matrices determine the dynamic properties of these models (e.g. species coexistence, temporal changes in abundance or responses to disturbance), but estimating these parameters from real communities is frequently daunting, if not impossible. Fortunately, some dynamic properties depend only on the structure, the skeleton, of the interaction matrix (i.e. on which species interact with which others). We illustrate how the concept of Strongly Connected Components (SCCs), that only requires knowledge of the structure of the interaction matrix, is useful to decipher relationships between structure, function and dynamics of complex systems. We focus our examples in models of plant communities driven by the replacement of individuals (replacement networks), but the framework can be applied to other ecological systems. Plant communities from Southern Europe, Northern Africa and North America share the same simple functional structure: a core of species benefiting each other and providing support for many other species. This structure can confer high long term persistence to the species in these communities, even after the eventual extinction of one of them.

2 Resumen

Los modelos de dinámica de sistemas ecológicos complejos incorporan una matriz que describe qué especies interactúan con cuales otras y cómo lo hacen. Los parámetros de esta matriz determinan las propiedades dinámicas del modelo (p. ej.: la coexistencia de especies, sus cambios de abundancia o su respuesta a perturbaciones), pero obtener estos parámetros en comunidades reales es extremadamente difícil. Afortunadamente, algunas propiedades dinámicas dependen solo de qué especies interactúan con cuales otras; es

decir, de la estructura, o esqueleto, de la matriz. El concepto de Componentes Fuerte-
mente Conectados (SCCs por sus siglas en inglés), que depende únicamente de la estruc-
tura de la matriz, permite relacionar estructura, función y dinámica de sistemas comple-
jos. Como caso de estudio aplicamos el concepto de SCCs a modelos de comunidades
de plantas basados en el reemplazamiento entre individuos (redes de reemplazamiento),
aunque puede aplicarse a otros sistemas ecológicos. Nuestros análisis de redes de reem-
plazamiento de Europa, África y América sugieren que éstas poseen el mismo tipo de
estructura funcional: un núcleo de especies que se benefician mutuamente y que propor-
ciona soporte para muchas otras. Esta estructura permitiría la persistencia a largo plazo
de la mayoría de especies, aún tras la extinción de alguna de ellas.

3 Community dynamics: lessons from a skeleton

In a broad sense, the study of community dynamics seeks to understand the temporal
patterns of change in abundance and composition of natural assemblages of species, and
the forces and mechanisms behind these changes. Thus, community dynamics addresses
fundamental questions about the structure [1, 2], function [3, 4] and stability [5, 6] of biodi-
versity. Natural assemblages of species are inherently complex systems, as they are com-
posed by a large number of elements (i.e. the species), each with different properties (i.e.
different life history), that interact with each other in different ways (e.g. through compe-
tition, predation, facilitation or mutualism). Because of this complexity, many questions
about the properties of these systems have only been addressed from theoretical, largely
mathematical, approaches [7, 8].

One key component of mathematical models of complex systems is the interactions
matrix (Figure 1A, B, C). Take for example the classical Lotka-Volterra models [9], Markov
chain models [10], or bioenergetic consumer-resource models [11]. In these matrices, the
diagonal elements describe intrinsic population properties of the species, such as their
population growth rate, birth and death rates, biomass density, mean individual size and
growth rate, the strength of intraspecific interactions, or the probability that the individ-
uals take hold of the space they occupy. On the other hand, off-diagonal elements of the
matrix indicate the strength or frequency of interactions between species (see Figure 1A,
B and C). Depending on the model, the values of the elements in the interactions matrix
can be constant, or they can vary deterministically with time, the environment or species
density, and/or they can vary stochastically.

Obviously, many important dynamic properties of community models depend on the
values of the elements of the matrix. For example, in the simple two-species competi-
tion Lotka-Volterra model, the stable coexistence of the species requires that the effect of
intraspecific competition in each species (i.e. the main diagonal elements of the interac-
tions matrix) is greater than the effect of interspecific competition with the other species
(i.e. the off diagonal elements of the interactions matrix), otherwise one of the species
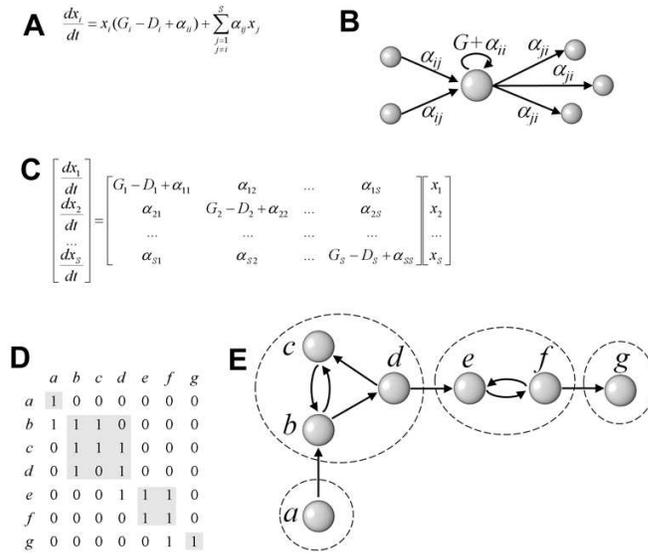
Figure 1: Different forms of expressing a mathematical model of community dynamics. A) Synthetic expression of a model of replacement dynamics in a community of competing species. The model contains a number S of species. The subindex i refers to the recruiting species, and the subindex j to the nurse species. The abundance (x) of each species varies with time as a function of its own abundance (x_i) and the balance between the vegetative growth rate of its individuals (G_i), their death rate (D_i), the rate of recruitment under conspecific individuals (α_{ii}), and the abundance of nurse species (x_j) and the rate of recruitment of species i under each nurse j (α_{ij}). B) The same synthetic expression can be represented as a simple graph of the inputs and outputs affecting a given component of the community. In this example, a focal species receives inputs of space from two nurse species and also gains some space through vegetative growth. When individuals of the focal species die, part of the space they occupied is passed to individuals of the same species or to individuals of other three species. If the system is at equilibrium, the death rate equals the sum of outputs from i. C) Representation of the model with explicit indication of the interactions matrix. D) Example of adjacency matrix showing the qualitative information of an interactions matrix with 7 species (a to g). The matrix is arranged in Lower Triangular Block Form. This arrangement is unique and places some non-zero elements of the matrix forming blocks along the main diagonal (shaded areas), and the rest of non-zero elements in the lower triangular side of the matrix. E) Replacement network derived from the adjacency matrix in D. The dashed circles indicate the Strongly Connected Components (SCCs) of the network. The SCCs of a directed network are groups of nodes in which resources, like biomass or space, can flow (directly or indirectly) from any node in the group to any other node in the same group, and back (i.e., resources can cycle between any pair of nodes within a SCC). In the example, there are two trivial SCCs (species a and g), one formed by two species ($e - f$) and one formed by three species ($b - c - d$). The SCCs correspond to the diagonal blocks of the adjacency matrix, and the links between SCCs are the non-zero elements in the lower triangular part of the matrix. Assuming that the SCC with three species is the "basic" SCC (see main text for a definition), then species b to g could coexist indefinitely because they belong to the basic SCC, or they recruit under some of its species directly (e recruits under d which belongs to the basic SCC) or indirectly (g recruits under f, which recruits under e, which recruits under d which belongs to the basic SCC). On the other hand, species a will eventually disappear because it does not recruit directly or indirectly under any species of the basic SCC. The interested reader can find further details in Alcántara and Rey [12].

becomes extinct. In this simple model, the community could finally reach three possible sets of stable species compositions depending on the relative values of the elements in the interaction matrix: species 1 only, species 2 only or the two species present. The more species there are in the model, the wider the set of stable community compositions possible. For example, with 10 species there are 1023 theoretically possible stable community compositions; the ones that actually occur in natural communities can only be ascertained through knowledge of the interaction matrix.

It remains an enormous challenge to obtain the information necessary to parameterize theoretical models with values from real communities [13, 14]. Setting aside the difficulties inherent to obtaining interaction parameters through field studies, the complexity of any community model grows exponentially with the number of species (S) because the number of parameters (i.e. interactions) in the matrix is S^2 (e.g. a model with 32 species involves a matrix with, at least, 1024 parameters). In fact, the few studies that have faced the challenge of parameterizing theoretical models with real world data have used the strategy of reducing the number of species by collapsing them through some type of aggregation, like grouping species by their trophic habit, size or any other relevant life history traits (e.g. [9], [15]).

Fortunately, some properties of the structure, function and stability of complex systems (e.g. biological communities) do not depend entirely on the exact values of the parameters of the interaction matrix. Interaction matrices contain two sources of information: quantitative and qualitative. Quantitative information refers to the exact values of the parameters in the matrix or the functions describing their variation, while qualitative information refers to the presence/absence of interactions (because not all possible pair-wise interactions do occur in real communities), their sign, and how they are arranged within the matrix. An interaction matrix parameterized with quantitative information contains also the qualitative information. Some aspects of the dynamics of a model depend more on the quantitative information but other properties depend more on the qualitative information contained in the interactions matrix [16, 17]. To fully understand the dynamics of the system we need to be aware of the contributions of each source of information.

The skeleton of the interaction matrix

To illustrate the utility of the qualitative analysis of complex systems, we will show how knowledge of the qualitative information of interactions matrices can be used to understand some important properties of the community. We will focus on replacement models of woody plant communities (e.g. shrublands and forests). These models consider that the change in species abundance in the community is driven by the replacement of dead individuals of a given species by individuals of the same or a different species growing beneath (see for example [18, 19]). This conceptualization of plant community dynamics as replacement systems can be traced back at least to [20], and has been recently advo-

cated by [21]. We have presented a detailed account of the theory and its application to replacement networks and food webs in [12].

The qualitative information, the skeleton, of a replacement model is a replacement network (Figure 1D and E) composed by populations of species forming a local assemblage. Each species is represented by a node in the network. There is an arrow from species j pointing to species i, indicating that individuals of species i recruit under individuals of species j (the nurse species) so if the individual of species j dies, the space it occupied can now be gained by individuals of species i. This convention makes replacement networks comparable to food webs where the arrows point from prey to predator, indicating the direction of biomass flow. In replacement networks the space (and the resources it contains) flows from the nurse to the recruiting species. A special node represents space not occupied by any plant (open space; e.g. a clearing in the forest), so some species can also recruit without the assistance (or without the interference or competition) of nurse plants. The graph representing the interaction network can be derived from its adjacency matrix, which is simply a binary version of the interaction matrix of the community model with the non-zero entries replaced by ones (ones in the adjacency matrix correspond to arrows in the network). Transforming the interactions matrix into an adjacency matrix means that we lose the quantitative information from the matrix but we retain the qualitative one. Nevertheless, it is far easier to obtain the information necessary to build the adjacency matrix of a real community than obtaining the information to parameterize the whole interaction matrix for the same community. In fact, the study of ecological networks based on the analysis of adjacency matrices has a long tradition and has flourished especially in the last decades [22].

Understanding the dynamical properties from the skeleton

Knowing the network's structure is not necessarily the same as understanding such structure. A key example of this problem is the issue of whether the species of an ecological network form compartments or modules. Identification of compartments in ecological networks is not merely a descriptive task: theoretically, compartmented systems have particular stability properties ([5, 23, 24]). Paradoxically, the search for compartments in ecological networks remains disconnected from the study of their dynamical properties, so even after finding compartments through some ordination procedure or modularity maximization algorithm [25], we would still be wondering whether such structures affect network dynamics. As stated by Dunne (2006): "There are likely innumerable ways for chopping up networks into clusters, but that does not mean that such clusters are necessarily meaningful for ecological function or dynamics."

To find out structures within the network that provide information about community dynamics we need first to realize that the network is part of a mathematical model of the community (Figure 1). In replacement models, like in any flow model that quantifies the interchanges of resources (e.g. biomass or energy flow in food web models), the

interaction matrix contains only zero or positive values (they are called "non-negative" matrices), and the corresponding networks are directed (i.e. the links between species indicate directions of flows so they are depicted as single headed arrows). The species in any non-negative directed network can be uniquely arranged into groups known as Strongly Connected Components (SCCs; Figure 1D,E). When applied to replacement networks, SCCs can be defined as groups of species such that the space occupied by individuals of one of the species can be occupied in the future by individuals of any of the species in the group. A SCC with a single species is called "trivial". Note that finding the SCCs requires only the qualitative information of the interaction matrix.

Since SCCs are groupings of species internally connected, they are useful to address questions related to the compartmentalization or modularity of ecological networks. Differently to most algorithms used to define modules in a network [25], the concept of SCCs has the advantage that there is only one way of partitioning a network into SCCs. In the replacement networks we have previously analyzed (10 from Southern Spain, 2 from Northern Africa and 3 from Mexico), the number of SCCs was very variable, but all the networks had a single large SCC and many trivial ones (Figure 2). So, according to their division into SCCs, replacement networks from three continents seem to share a common structure: a "core" of species recruiting directly or indirectly under each other, and a large set of "satellite" species linked to it. This structure indicates that woody plant communities have very low modularity (single species cannot be considered a compartment or module). Although it is still premature, it is tempting to ask why this particular structure arises in such different communities.

To begin with, this structure is different from the configuration expected if the recruitment interactions were randomly determined: at the density of interactions found in replacement networks, a randomly assembled network would form a single SCC grouping all the species [27]. Our next step seeks a functional interpretation of the network structure. We will start by assuming, as it is common in community dynamic modeling and ecological network analysis, that the qualitative structure of the replacement network remains constant (but see [28]): the zero elements of the matrix remain zero (i.e. some species will never recruit under others) and the positive elements remain non-zero although their value may not be constant. We also need to define the "basic" SCC of a network: mathematically, an SCC is called basic if its largest eigenvalue is the largest eigenvalue of the matrix. Although we would need quantitative information to ascertain which one is the basic SCC, in replacement networks it will usually be the one with the largest number of interactions (which will likely be the one formed by more species). According to matrix theory, when a system contains several SCCs, the species that can coexist are those forming the basic SCC and those that can recruit directly or indirectly under the species of the basic SCC [29]. This simple theorem explains the importance of SCCs, and how they are arranged, for the persistence of species in a replacement network [12]. Based on this theorem we can see that the structure we have found in replacement networks can allow a large proportion of species (83% on average) to coexist in the long term
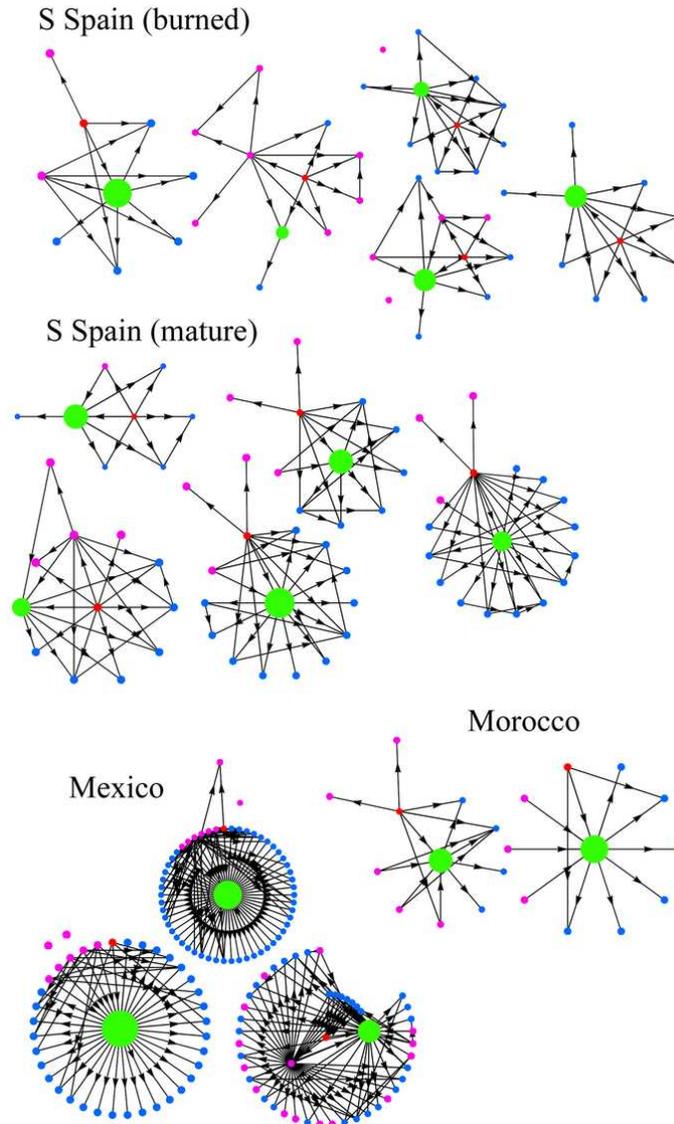
Figure 2: Examples of replacement networks from Southern Spain [12], Southern Morocco (Rey and Alcántara unpublished data) and Mexico [26]. Each node represents a SCC. The green SCC is the only non-trivial one in each network, and its size is proportional to the number of species it contains; it forms the "core" of species in the network. The blue and purple nodes are trivial SCCs (i.e. SCCs formed by a single species each) that can be considered as "satellite" species, related but not included in the core. The red node represents space not covered by any nurse species. Assuming that the green node is a basic SCC (see main text for a definition), the species in the green and blue nodes could coexist, but the species represented by purple nodes would eventually disappear from the local community.

because most of them are integrated in the core SCC and those that are not, are nevertheless able to recruit under some species of the core. Still, an average 17% of species in these communities seem deemed to local extinction. Moreover, we can also infer that replacement networks are quite robust after the extinction of one species. On average, the extinction of one species would lead to the subsequent extinction of no more than 5% of species. Noticeably, this high robustness to species extinction seems to emerge from the low modularity of these species interaction matrices.

In conclusion, the skeleton of the interaction matrix, when considered as part of a community dynamics model, can provide important insights about community structure, function and stability. Although many more study cases are required to conclude about general patterns, the scarce replacement networks available suggest that local woody plant communities may have a simple functional structure with most species forming a core of interactions that supports most of the rest of species. This structure can confer the species in these communities a high probability of persistence in the long term, even after the eventual extinction of one of them.

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